

THE SELECTIVE VALUE OF AESTIVATION AND HIBERNATION IN A CALIFORNIA BUTTERFLY.

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Some notes and observations on the phenomenon of aestivation and hibernation in some western races of *Melitaea phaeton* will be described and discussed in this paper.

Hibernation and aestivation are usually considered as torpid states of animals, developed for the purpose of enabling the animals to withdraw as far as possible from an unfavorable environment without actual migration. In regions where most of the research upon this phenomenon has been performed, the winter season presents the unfavorable environment and the studies have been made, therefore, on hibernation. In arid or relatively arid regions, however, the entire season between wet periods may be unfavorable for many forms. At the lower elevations in California, this season extends from the end of the spring rains (April, May or June) until the next December or January. The temperature throughout the entire year is essentially mild, though the winters in the north are cold for a short period and the summers in the southeastern deserts become rather hot. For many butterflies whose larval food-plants grow only during the rainy season this means a continuous, combined aestivation and hibernation from May or June until the next January or February.

The races of *Melitaea phaeton* in California (the *Euphydryas chalcadona* and *anicia* variations of some taxonomists) present some interesting problems. The life-cycle of this insect is so arranged that it can exist only in areas where its food-plant is in green, growing condition (not "leathery" like many desert species get in dry seasons) for a period extending through the entire life-cycle of the butterfly (not only during the larval life). The species aestivates as a quarter-grown larva at the base of or near the food-plant. In the spring (February at low elevations), the larvae begin feeding again; the food, of course, must be green at this time. After a period of feeding, they pupate and later emerge as adults. These adults normally lay eggs upon the tips or upon the uppermost leaves of the growing plant and these eggs hatch in about a week. The plant at this period, also, must be green and fresh because the larvae must feed and grow for some time before aestivation sets in. Although in the case of *Argynnis* the young larvae will hibernate without first feeding, unpublished experiments have shown that young

Melitaea larvae will die at this time if not fed. The larvae will feed until about one-fourth grown and will then go into a stupor from which it has not been possible as yet to immediately awaken them. In the coastal area of California, the food plants of the species (*Scrophularia californica*, *Diplacus* spp., and *Pentstemon cordifolius*) are green and are in good condition as food from January until June in normal years. In central California the larvae are first found upon the plants in early February, adults emerge in April and May, and the second generation larvae disappear in late May and early June. In the Mohave desert of southeastern California the food plant of the species (*Pentstemon antirrhinoides*) is usually green from March until May. The active part of the life-cycle of the *Melitaea* is correspondingly shortened (genetically, as shown by preliminary laboratory experiments).

Some inquiries into the ultimate cause determining the onset of the diapause seem to be leading the author to consider the phenomenon in *Melitaea* as of entirely genetic origin. Of the environmental conditions in the wild, none seem to be of sufficient importance to directly cause it. The plant may be green with plenty of fresh leaves, the air may be humid, the temperature not too hot and yet the larvae aestivate. It is the same in the laboratory; no amount of food can induce the larvae to continue to feed. Since it was found that neither temperature nor moisture had any effect, an experiment was performed to see if length of day had any. Larvae from wild eggs were grown, half at an eight-hour day and half at a fourteen-hour day (temperature and humidity being kept constant and identical in both cases). Except for the fact that those larvae at fourteen-hours hibernated first, there was no difference in the reaction. Possibly, had the eggs not been allowed to remain in the wild until they hatched, the results might have been different; this will be studied further in the future. More evidence for the supposition that hibernation is independent of the environmental conditions in this species lies in the fact that out of each brood of wild larvae bred in the laboratory, a certain small proportion never reach the pupal stage with the others but will go into an aestivation or hibernation period which would correspond in the wild to two years or more of diapause. Likewise, in a cross between an isolated Mohave desert population and a coastal population (data kindly supplied by C. M. Dammers, from unpublished experiments) the hybrids gave an extremely mixed relationship such as would be expected with the mixing and reshuffling of all the probable genes responsible for the phenomenon. Unfortunately, numerical counts were not made of

the hybrid reactions. However, it was found that many larvae hibernated one year as normal but others hibernated and aestivated for two, three, four and some are still going on the fifth year. All larvae were treated alike and fed well.

The selective value of hibernation and aestivation is decidedly easy to visualize. Any larvae which failed to aestivate would soon perish. Even if the food did not dry up before pupation, the newly-hatched larvae of the following generation would certainly perish. Individuals homozygous for genes responsible for the failure would, thus, be eliminated within that generation or in the early part of the next. Genes responsible for diapause of more than two years would be favored in one sense and be at a disadvantage in another. Being in an immobile state for any length of time is disadvantageous to any living thing and conducive to rapid elimination. Also, the food stored in the body is not inexhaustible even though the metabolic processes are at a slow rate. Elimination could, therefore, result from either starvation or destruction by environmental factors. In cases where any season's generation may be eliminated by causes due to parasitism, death or drying-up of the food-plant, etc., the individuals hibernating for more than one year will be greatly favored; upon them will depend the continuance of the population. Such a situation is not so far removed from the possible as may be supposed. Ford and Ford¹ describe a case in which a population of *Melitaea aurinia* (an English form) was very abundant but became so heavily parasitized that it became extinct except for one or two observed individuals per year. It was noted that there was a high frequency of aberrations in phenotype at the time when the population began to rebuild itself; these would result either from an increase in unfavorable gene combinations or mutations, or from a lesser destruction of these by natural selection. If the population had to rebuild itself with the material which had hibernated for more than one year, such a situation might be explained by the fact that these individuals were physiologically aberrant to begin with. Their genotype was not normal and hence it would be expected that a large percentage of aberrant phenotypes would be produced. Goldschmidt has shown that an only slightly unbalanced genotype can create havoc with the timing of pattern and color formation. In this case, many generations would be necessary to balance the many genes controlling hibernation and other life processes in the same or in a possibly changed

¹ Ford, H. D., and E. B. Ford. 1930. Fluctuations in numbers, and its influence on variation, in *Melitaea aurinia* Rott. (Lepidoptera). *Trans. Entom. Soc. Lond.*, 78: 345-351.

environment. Ford and Ford have shown the latter to be the case with respect to the phenotype in the population they had under observation.

Occasionally an autumn generation of this species (*M. phaeton*) is produced in the Mohave desert after a rare rain at that time of the year. It is not known whether this generation is eliminated by unfavorable conditions or actually produces offspring which appear the next spring. There is some evidence to believe that it is eliminated, however, because in one observed case large numbers of dead pupae were found upon the food plant, killed perhaps by the sudden approach of cold weather in winter. It may be that such generations are drains upon the life of the population as a whole. Presumably, therefore, hibernation in this species is not entirely controlled by the environmental conditions nor is it a "time-switch" utterly independent of the environment, but rather a procedure which stops development at a not-yet present danger period and then, when favorable conditions again appear to be present, allows the larvae to continue to develop.

Compendium of Entomological Methods—Part II—Orthoptera, by Irving J. Cantrall and others. Pp. 1-26 and figures not numbered. Ward's Natural Science Establishment, Rochester, N. Y. 1941.

As Ward's say in the title-page, this pamphlet is "published in the service of entomology." It is one of those needed things of which there are so sadly few. Collecting of all kinds is largely a matter of personal experience; and every set of directions for any given order is always to be construed in the light of such experience. Still, anyone of us, no matter how great his experience, is always finding new situations or conditions distinct from what has gone before. Now, Dr. Cantrall's Notes add materially to Banks' old "Directions"; they are specific and plain. Starting with the collecting apparatus, the Notes end with ways of keeping records and studying living specimens.

Of course, every reader and user of these Notes who collects Orthoptera has his own pet methods and gadgets, but it never yet hurt anyone to know how the other fellow does it. Even hard-boiled heteropterists may con this useful paper with profit.

And Ward's is to be congratulated on producing this "Compendium."

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